



An Ordination of the Upland Forest Communities of Southern Wisconsin

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Source: *Ecological Monographs*, Vol. 27, No. 4 (Oct., 1957), pp. 325-349

Published by: Wiley

Stable URL: <http://www.jstor.org/stable/1942268>

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AN ORDINATION OF THE UPLAND FOREST COMMUNITIES OF SOUTHERN WISCONSIN*

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INTRODUCTION

A renewed interest in objective and quantitative approaches to the classification of plant communities has led, within the past decade, to an extensive examination of systematic theory and technique. This examination, including the work of Sorenson (1948), Motyka *et al.* (1950), Curtis & McIntosh (1951), Brown & Curtis (1952), Ramensky (1952), Whittaker (1954, 1956), Goodall (1953a, 1954b), deVries (1953), Guinochet (1954, 1955), Webb (1954), Hughes (1954) and Poore (1956) has accompanied theoretic studies in taxonomy [Fisher (1936), Womble (1951), Clifford & Binet (1954), Gregg (1954)] and in statistics (Isaacson 1954). It is a conclusion of many of these studies that nature of unit variation is a major problem in systematics, and that whether this variation is discrete, continuous, or in some other form, there is a need for application of quantitative and statistical methods. In ecologic classification, an increased use of ordinate systems, which has been stimulated by the development of more efficient sampling techniques and the collection of stand data on a large scale, has prompted the proposal of the term "ordination" (Goodall 1953b). Goodall (1954a) has defined ordination as "an arrangement of units in a uni- or multi-dimensional order" as synonymous with "Ordnung," (Ramensky

1930), and as opposed to "a classification in which units are arranged in discrete classes." The present study is an attempt to examine the upland forests of southern Wisconsin in relation to a suspected multidimensional community structure by the use of ordination method and in so doing, to review the theoretic position necessary to such an examination.

LITERATURE REVIEW

The application of quantitative techniques to community classification has been based, in part, upon the assumption that quantitative community composition, as determined by suitable sampling methods, can be a primary basis for the building of ordination systems. This assumption was emphasized by Gleason (1910) in an examination of the relationship between biotic and physical factors. Gleason quoted Spalding (1909), "The establishment of a plant in the place which it occupies is conditioned quite as much by the influence of other plants as by that of the physical environment," and concluded from his own observations, ". . . the differentiation of definite associations is mainly due to the interrelation of the component plants; and the physical environment is as often the result as the cause of vegetation." Further emphasis upon vegetation in itself was made by Clements & Goldsmith (1924), and more recently, by Mitsudera (1954), who regard the community as an instrument which, if properly examined and manipulated, might be a key to the relation of biotic and physical phenomena. Cain (1944), Goodall (1954a, 1954b), Whittaker (1954) and Williams (1954) have questioned the relevance of considering single physical environmental factors apart from an environmental complex. Insistence upon the study of vegetation on

* This work was supported, in part, by the Research Committee of the Graduate School of the University of Wisconsin, from funds supplied by the Wisconsin Alumni Research Foundation.

The Junior F. Hayden Fund of the University of Minnesota provided partial support of publication costs.

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its own level has been reiterated in many studies with recent examples in Shreve (1942), Curtis & McIntosh (1951), Brown & Curtis (1952), and Ramensky (Pogrebnjak 1955).

Included in information on community structure are two basic relationships: that of individual species to each other, and that of stands or plots as a whole to each other. These relationships have determined the development of two complementary but separate approaches to the problem of classification.

The species approach stresses the degree of mutual occurrence of a species with other species. This approach received an early quantitative background in the work of Forbes (1907a&b, 1925) who proposed a coefficient of associate occurrence which he applied to the study of bird and fish communities. Further development of the concept of associate occurrence led to the elaboration of indexes of interspecific association (Dice 1948; Cole 1949; Nash 1950) and to the construction of indexes of relative species occurrence (deVries, 1953, 1954; Bray 1956a). Indexes of interspecific association have been applied, in classification, (1) to correlate species with host specificity or with environment (Agrell 1945; Hale 1955), (2) to determine community groupings by the selection of groups of species with high interspecific correlations (Stewart & Keller 1936; Tuomikoski 1942; Sörenson 1948; Goodall 1953a; Hosokawa 1955-1956) and (3) to determine degree of amplitudinal overlap of species as an indication of kind of community variation (Gilbert & Curtis 1953). Indexes of relative species occurrence have been used as the basis for a spatial ordination of the species (deVries 1953, 1954) or for an objective assignment of species adaptation values (Bray 1956a).

The second basic approach, that of correlation among stands as a whole, can be roughly divided into three methods. The first uses information other than that derived from the vegetation in order to establish a primary series of gradients or regimes along which a subsequent vegetation alignment is undertaken (Wiedemann 1929; Vorobyov & Pogrebnjak 1929; Pogrebnjak 1930; Ramensky 1930; Hansen 1930; Whittaker 1956). These regimes do not usually represent direct physical environmental factors, but more often express environmental complexes of interrelated factors, such as soil moisture, or they follow environmental controls, such as elevation, which determine a complex of factors. Ramensky, for example, used previously established soil moisture and soil nutrient regimes to construct a primary stand ordination from which "Functional Averages" were extracted by a series of eliminations of aberrations in the compositional stand data. These averages were considered the median conditions of the biocoenosis and served as bases for final stand orientation. The work of Ramensky included some of the first intergrading bell-shaped species distributions to be demonstrated along vegetational gradients.

The second stand method is the use of objective techniques to show relationships among stands which

have previously been classified into discrete units, usually within the Braun-Blanquet system. This use was given an early formulation in the work of Lorenz (1858) who was apparently the first to apply quantitative methods in community classification when he compared various kinds of moors on the basis of "per cent of species similarity." Later techniques, including those of Kulczyński (1929), Motyka *et al.* (1950), Raabe (1952) and Hanson (1955) use Jaccard's Coefficient of Community or one of its quantitative modifications to show the compositional similarity of units on various hierarchical classification levels.

The third method attempts, from a direct analysis of quantitative vegetational data, to demonstrate degree of relationship by the construction of compositional gradients which are independent of environmental or other considerations. The use of the various techniques of factor analysis (Goodall 1954b), of stand weighting devices based on the assignment of species adaptation values (Curtis & McIntosh 1951; Brown & Curtis 1952; Parmalee 1953; Kueera & McDermott 1955; Horikawa & Okutomi 1955), and of attempts to utilize directly indexes of quantitative coefficients of community (Whittaker 1952; Bray 1956a) or indexes of occurrence probability (Kato *et al.* 1955) are examples of the above approach.

PREVIOUS TREATMENT OF THE UPLAND FOREST OF WISCONSIN

A linear ordination of the stands of the upland forest of southern Wisconsin was presented by Curtis & McIntosh (1951). Subsequent studies were made in which soil fungi (Tresner *et al.* 1954) were arranged along this ordination and in which corticolous cryptogams were related in part to the ordination and in part to host specificity (Hale 1955). Other studies were made of the forest herbs (Gilbert 1952), of autecological characteristics of herbs (Randall 1951), and of the savanna transition into prairie (Bray 1955).

Limitations to a linear presentation became apparent from continued Wisconsin field work. One was the observation of ecological substitution in which two separate species alternated in sharing what appeared to be identical ranges of environmental tolerance (McIntosh 1957). Further reason to suspect the existence of a possible multidimensional structure came from a growing realization of the importance of past history in determining the composition of any stand.

SOURCE OF DATA

All of the 59 stands of this study were sampled by the same methods. The trees were measured by the random pairs technique (Cottam & Curtis 1949) using 40 points and 80 trees per stand. The characters here used are absolute number of trees per acre and total basal area per acre, both on a species basis. The shrubs and herbaceous plants were sampled by 20 quadrats, each 1 m. sq., laid at every other point. The character used is simple frequency.

The stands employed were selected from the large number available by a stratified random procedure, so devised as to give an equal number of stands from each major geographic portion of the southwestern one-half of Wisconsin. All stands were at least 15A in size, were on upland sites upon which rain water did not accumulate, and were in reasonably undisturbed condition. As actually applied, this last criterion meant that the stands were ungrazed, had not been subject to fire within the recent past, and had never been logged to such an extent as to create large openings in the canopy. In most cases, a few trees had been removed at various intervals in the past, as witnessed by an occasional stump. The limited logging probably created serious errors in the measured amounts of *Juglans nigra*, since this high-value species was deliberately searched for on an intensive scale during World War I. It is believed that the population densities of the remaining species did not vary greatly from those which would normally be produced by natural death and windthrow. A very few stands were totally undisturbed for at least the past 50 yrs.

The sampling methods employed for both the trees and the understory were not, as could be expected, completely free from error. Estimates of sampling error were made by repeated sampling of the same stand, using different investigators in both the same and in different years. Two extensive series of such tests, in a maple woods and an oak woods, showed a standard error of 10.8% for the individual tree species and 7.1% for the understory plants. On this basis a conservative estimate of over-all error in the individual stand measures of about 10% seems reasonable. Obviously, this error would be much less for the most common species and greater for the rare species (Cottam *et al.* 1953).

We are indebted to Dr. Orlin Anderson, Dr. R. T. Brown, Dr. Margaret L. Gilbert, Dr. George H. Ware, Dr. Richard T. Ward, and especially to Dr. R. P. McIntosh for their aid in the collection of the original data. Professor Grant Cottam of the University of Wisconsin and Professor J. W. Tukey of Princeton University were very generous with their time and advice on various problems.

Taxonomic nomenclature in the present paper is after Gleason (1952).

TREATMENT OF THE DATA

NATURE OF THE APPROACH

The ordination approach was selected for the present study in order to provide statements (1) which depict, with a sufficient degree of quantitative exactness, the compositional structure of a community and (2) which might be able to give some initial indication of the over-all patterns of interaction between biologic and physical phenomena. The possibility of using ordination statements to suggest causal reactions is dependent on the concept of physical and biotic factors interacting in a relationship in which each factor is, to some degree, mutually determined

by the others. There is, therefore, as is often noted in ecologic writing, no simple cause and effect relationship between physical phenomena (as primarily causal) and biotic phenomena (as primarily effectual), especially in the more complex environments. There is, rather, instead of a domain which is determined by a small number of independent factors (that is, a system of mechanist causality), a field of interrelated units and events (configurational causality). The ordination of this field is, then, a plotting of the changes in some biotic and/or physical features from area to area within the system, or, in another sense, a mapping of its complexity. Such a mapping indicates, by the relative proximity of different features and their varying spatial patterns, the degree to which the features may participate in a mutually determined complex of factors. With the completion of this mapping, it may then be possible to apply statistical tools which indicate more fully the causal interactions in any one part of the ordination.

Of the two major approaches to ordination study, that of stand or of species orientation, it was decided to use a technique which gave theoretic spatial relations of stands as a first result. With such a framework, the distribution patterns of individual species can be easily studied by directly plotting some measure of their behavior in each stand. A similar plotting can be made for measures of environmental or historic factors in each stand, or for general descriptive features. If the ordination is originally based upon species rather than stand relationships, then the location of relative stand position (and as a consequence, correlation with environmental features) becomes more difficult.

USE OF SCORE SHEETS

If the degree of similarity of stands, one to another, is to be assessed, then some decision must be made as to what criteria are to be used in judging this similarity. There is wide agreement amongst temperate-zone ecologists that community comparisons must be made on a floristic basis and that environmental or other features are not valid for primary comparisons. Unfortunately, this agreement does not extend much beyond the general idea of floristics. Clements and the Anglo-American school generally recommend the use of the dominants as the main criterion of community or stand relationship, while Braun-Blanquet and his adherents use characteristic species of high fidelity, even though these may be small, rare or otherwise dynamically insignificant members of the assemblage. Lippmaa (1939), Daubenmire (1954) and others use synusia, either singly or in combination, for their characterization of community resemblance. In no case has the total flora of a given stand been used, since the determination of all of the bacteria, soil fungi, soil algae, liverworts, mosses, lichens and vascular plants is usually beyond the facilities at the command of ecologists. The principle is well recognized, therefore, that the entire species complement is not needed for meaningful statements about community composition. The disagreement lies

in the question of where to draw the line short of the total flora.

In the similarly complex problem of soil classification, it is possible that the degree of resemblance between a series of soil samples might be determined by applying a single test to each sample. Such tests might measure the texture of the soil, its percentage content of sand, or some other simple character. It would then be possible to arrange the group in descending order, as from very sandy through sandy-loam to non-sandy. The sandy loams in the center would have certain features in common and would differ greatly from the two extremes, but they might well include soils which differed widely among themselves. The application of a second test to the samples, such as fertility level, would serve to differentiate soils which were of similar texture, but, even so, the resulting groups might not be homogeneous—they might differ in organic matter content, pH, color, or other characters. A similar problem was recognized by Pirie (1937), "In an earlier part of this essay the transition from living to non-living was compared to the transition from green to yellow or from acid to alkaline. If this comparison were valid, it would be possible to lay down a precise but arbitrary dividing line. But as it has been shown that "life" cannot be defined in terms of one variable as colours can, the comparison is not strictly valid and any arbitrary division would have to be made on the basis of the sum of a number of variables any one of which might be zero." The best approach might therefore be to apply a series of tests, each examining some pertinent or important aspect of soil makeup. A study of the results of the series of tests would give a firm basis for comparison of the original group and would easily pick out the soils most nearly related to each other and least closely related to others. It might be desirable to weight the test results, in order of their importance. The calcium content is more important than the sodium content in most temperate forest soils and its results might be appropriately weighted to show this importance. Statistically, the degree of relationship could be shown by a suitable measure of the correlation between the sets of test values for any two soil samples.

The same procedure can be employed in the floristic analysis of plant communities. A standard series of tests can be applied to each stand and the results for pairs of stands correlated with each other. If this is done for all stands in the series, then similar stands should have high mutual correlation values, but dissimilar stands should show low correlation. If an appropriate measure of correlation is used, then the resulting index should give a linear measure of the difference between any two stands.

One test of the similarity of two stands could be the quantity of *Acer saccharum* that each contains, analogous to a determination of the calcium content of soil samples. A series of such tests, using other dominants, would increase the precision of the com-

parison. Similarly, a series of herbs and shrubs, chosen to include some which were restricted to the formation under study and others known to be sensitive to the varying conditions present in different stands of the formation, could be added to the list of tests.

In the current studies, measurements of 26 species were used as the tests. Twelve of these species were dominant trees, while the remainder were herbs and shrubs. The trees included all of the species with a presence value above 33% in the 59 stands studied. The herbs and shrubs were chosen at random in blocks along the original continuum gradient from among those species which were neither overly common nor rare and which had shown clear cut distribution patterns in previous studies. Weighting of the 12 dominant tree species was accomplished by using two separate measurements of each species (absolute density per acre, and absolute dominance per acre) as independent tests.

There were, thus, 38 tests employed for each stand: frequency (in 1 m quadrats) of 14 species of herbs and shrubs, density of 12 species of trees, and dominance (in square inches of basal area at breast height) of the same 12 trees. The results of the tests for each stand were recorded in a separate score sheet for that stand. (Of course, many of the test scores on a given sheet were zero, when one or more test species was missing from that stand.) The test scores were in different units, since the original measurements were made in three different classes. This discrepancy was rectified by expressing each score as a percentage of the maximum value attained by that test on any of the sheets. These corrected scores thus indicated, in comparable units, the behavior of each test species in relation to its optimum behavior in the entire series. Since the number of test scores and the sum of these scores varied from stand to stand, the scores for each stand were adjusted to a relative basis. They finally indicated, therefore, the relative amount contributed by each test organism to the combined score for the stand. In one stand, for example, species A may contribute 17.1% of the total score while species B may represent only 1.9%. The adjusted scores on a relative basis appear to offer the best basis for making comparisons between stands (Whittaker 1952).

INDEX OF SIMILARITY

The choice of a suitable index is largely dependent on the choice of an ordination technique. There are, however, several characteristics of available indexes which should be examined. The standard correlation coefficient, "r," incorporates a square transformation which leads to the weighting of the importance of entries with high values. Thus, if a pair of stands have one or two species in common which have high score values, the stands will have a high correlation coefficient regardless of the relative similarity or dissimilarity of their lesser species. It can be shown that high values of "r" cover a wide range in interstand variation and are relatively insensitive in

the medium to high areas of stand similarity. There is a high sensitivity in the lower range of coefficient values of "r," but this sensitivity lies in an area where the ecologic differences between stands are not very significant due to the residue of widely plastic species which inhabit many of the stands of any geographic area. Of the available indexes of similarity employed in phytosociology, both Gleason's quantitative modification of Jaccard's Coefficient of Community (Gleason 1920) and Kulczyński's index (1927) can be shown to have a greater ability to differentiate stands within the area of medium to high similarity than has the correlation coefficient. When the sum of score values is relative and equals 100, both Gleason's and Kulczyński's coefficients can be expressed in the terms later used by Motyka *et al.*

(1950) as $C = \frac{2w}{a+b}$ where a is the sum of the quantitative measures of the plants in one stand, b is the similar sum for a second stand, and w is the sum of the lesser value for only those species which are in common between the two stands (Oosting 1956).

Thus, if two stands by chance had exactly the same scores for exactly the same species, the index would be 1.00, since (a) and (b) would be equal and both would equal (w). If there were no species in common, then the index would be zero. The range from no resemblance to complete identity is appropriately covered by the range from 0 to 1. This index appears to be the best approximation yet available to a linear measure of relationship.

As used in the present study, the index reduces simply to (w), or the sum of the lesser scores for those species which have a score above zero in both stands. This is due to the use of relative scores, such that (a) plus (b) is always 2.00 in every pair of stands and $\frac{2w}{2.00} = w$. In practice, the score sheets

were so arranged that the final adjusted scores were recorded in the last column on the extreme edge of the sheet. One sheet could then be superimposed, in turn, on every other sheet in a slightly offset position, and the lesser values added on a machine for all tests where a positive value was present on both sheets.

When a large number of stands are studied, the calculation of the w index becomes burdensome, since there are $n \times \frac{n-1}{2}$ comparisons to be made. Thus, for 10 stands, 45 comparisons are needed, while for 100 stands, 4950 are required. In such cases, recourse should be had to electronic calculators, using punch cards as score sheets. In the present case, a complete comparison was made by hand for 59 stands, resulting in 1711 values of the w index. These values were arranged by stand number in a matrix. We would be happy to correspond with anyone who is interested in obtaining a copy of the matrix for further work.

THE ORDINATION METHOD

The use of stand data and of a summation of a series of tests of these stands has been outlined as the quantitative basis for the present study. Of the ordination techniques which were reviewed, many depend upon the use of a previous knowledge and sometimes classification of either the vegetation or physical environment. Although this use is not necessarily undesirable in ordination studies, it is apparent that a technique which can extract an ordination directly from the available data would be best suited to the present study. One quantitative and completely objective technique which makes this extraction is factor analysis.

Factor analysis seeks to draw "functional unities" (factors) from an oriented table (i.e. matrix) of correlation coefficients. These coefficients can be calculated, as in Goodall (1954b), from a correlation among species, which are correspondent to tests in factor analysis; or, if the relationship among stands is needed, the use of direct interstand correlation is permissible (Tucker 1956). In either case, the standard techniques of factor analysis are applicable. The extraction of a functional unity is followed, in most factor techniques, by the computation of a new matrix, called the residual matrix, from which the next unity can be obtained. This series of extractions results in a number of linear vectors, called the factor matrix, and an attempt is then made to identify each vector with an underlying cause. Factor analysis is used in areas where no hypotheses are available about the causal nature of the domain, and is based upon the assumption, according to Thurstone (1947), that "... a variety of phenomena within a domain are related and that they are determined, at least in part, by a relatively small number of functional unities or factors." When applied to ordination study, however, these functional unities are not, as is emphasized by Goodall (1954b), direct environmental forces but are rather, sociologic factors. A sociologic factor is defined as "an element in the description of the composition of the vegetation," and it may or may not be related to environmental factors.

The application of factor analysis to the present study was carefully considered, but was rejected for the following reasons: (1) the heavy computational load involved in handling 59 stands, (2) the disadvantages, which have been discussed above, in applying "r" (the correlation coefficient) to stand data, and (3) a hesitancy in interpreting factor analysis when applied to stand data especially in regard to the difficulties noted by Goodall (1954b), "though the factors may be statistically orthogonal, they are not biologically independent; the interpretation thus becomes more complicated." The construction of a preliminary empiric method with the following criteria therefore seemed desirable: (1) vegetation structure is regarded as a possible key to the nature of the interaction of factors, and, as such, must be studied on its own level, (2) an extraction of

an ordination directly from objectively derived data without previous classification would be desirable.

The basis of a technique which might satisfy the above criteria is the same as that for ordination systems in general: the degree of phytosociologic relationship between stands can be used to indicate the distance by which they should be separated within a spatial ordination. The degree of relationship of vegetation units has usually been measured by some estimate of the similarity of stand composition, with a high degree of similarity signifying a close spatial proximity. The technique which will be outlined attempts, therefore, to extract from a matrix of measurements of interstand similarity, a spatial pattern in which the distance between stands is related to their degree of similarity.

Given a matrix of values of distance between points in Euclidean space, it is possible, without a prior knowledge of their location, to reconstruct their spatial placement (Torgerson 1952). This reconstruction depends upon simple techniques in which, in two dimensional space, for example, 3 points not in the same location and not on the same line, are used to locate the other points by their relationship to the 3 reference points. If, for example, there were in a matrix, 4 points, of which A, B, and C were each separated by a distance of 40 units and point D was separated from A and B by 20 units and from C by 34.64 units, then the position of these points could be established, with A, B, and C forming the apices of an equilateral triangle and D occurring midway on line AB.

When coefficients of community are used, however, as indicators of spatial distance, then exact interstand distances are not available, since the position of a stand in relation to another stand occurs within an area of uncertainty originating in the sampling error made in surveying the stands. Furthermore, it is likely that stands occupy proximate instead of exact theoretic positions in relation to each other. The occurrence of stands within an area of uncertainty results in a matrix of estimated proximate distances. If such proximate distances are available, then the location of stand D in the previous example might be in a different position relative to reference stands A, B, and C as compared to three other reference stands (if exact interstand distances were available, the positions would be the same regardless of the choice of reference stands). The technique to be developed, therefore, is a preliminary attempt to derive an ordination from estimates of proximate interstand distance which gives a single spatial configuration most closely approximating the matrix distances.

This technique depends upon the selection of a pair of reference stands for the determination of stand positions on any one axis. Given proximate interstand distances, the choice of reference stands is of crucial importance. In making this choice, it is evident that reference stands are comparable, in part, to sighting points as used in plane-table surveying

and that those stands which are furthest apart will be more accurate for judging interstand distance than those which are in close proximity. This accuracy is especially desirable because of the area of uncertainty in which each stand fluctuates relative to the positions of neighboring stands. If these fluctuations are greater than the actual distance apart of the reference stands, then the resulting ordination will reveal only these fluctuations. It is necessary for any ordination that the sphere of fluctuation for any stand be small in relation to the space occupied by the ordination as a whole. The choice of reference stands should be, therefore, of those stands which are furthest apart and as a consequence, have the greatest sensitivity to over-all compositional change.

AXIS CONSTRUCTION

The ordinate location of points in space by the use of reference stands is illustrated by the ordination of five points whose hypothetical interstand distances are shown in the lower-left of Table 1. The distances, although hypothetical, represent exact spatial distances. They were determined by inverting the estimates of stand similarity which appear in the upper-right of the table so that a high degree of similarity was represented by a low degree of spatial separation. The inversions were accomplished by subtracting each index of similarity from a maximum similarity value of 100.

To locate stands between a pair of selected reference stands, a line connecting the reference stands is drawn to scale on a piece of blank paper, and the position of every other stand is projected onto this line. The projection is accomplished by rotating two arcs representing the distance of the projected stand from each of the reference stands, and then projecting the point of arc intersection perpendicularly onto the axis. Applying the criterion of the greatest degree of spatial separation as determining the choice of reference stands, Table 1 shows stands number 1 and 2 to have a maximum separation of 99.9 units. These stands were selected, therefore, as the x axis reference stands and are placed in Fig. 1 at a distance of 99.9 units. Stand 3 in Table 1 is 70 units from reference stand 1 and the same distance from reference stand 2. Stand 3 is located in Fig. 1, therefore, at the intersection of arcs with radii of 70 units and bases at points 1 and 2. Two such intersections are possible in a two dimensional ordination, and the points of intersection are projected perpendicularly onto the x axis, as shown in Fig. 1, to give an x axis location of 50 units. Stand 4 can also be located along the x axis by the arc intersection and projection technique; it occurs at 62 units along the x axis. Stand 5 is similarly located, after intersection and projection, at 62 x axis units. It can be proven geometrically that a constellation of points in n space can be projected perpendicularly onto the line connecting the two reference points which are furthest distant in the constellation by using the above technique.

TABLE 1. Matrix of hypothetical exact interpoint distances. The upper-right portion of the table shows hypothetical data on point similarity for an exact spatial system. The lower-left portion shows data on similarity which were inverted to show interpoint distance.

Stand No.	1	2	3	4	5
1.....	...	0.1	30	30	30
2.....	99.9	...	30	50	50
3.....	70	70	...	17.8	79.6
4.....	70	50	82.2	...	35.2
5.....	70	50	20.4	64.8	...

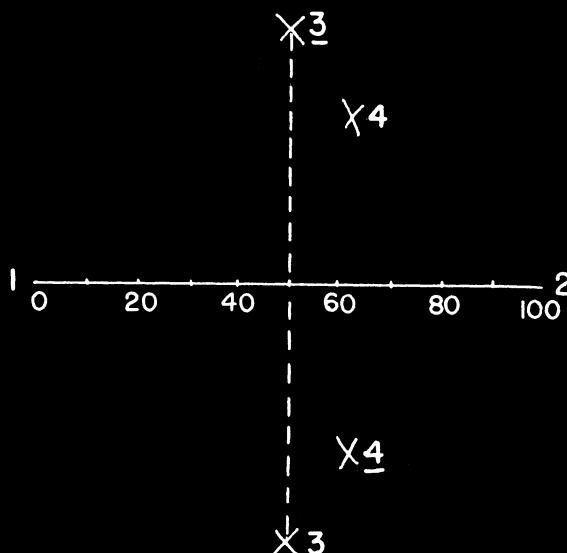


FIG. 1. Demonstration of stand location by the intersection and projection technique. Stand 3 is located at the intersection of arcs with radii of 70 units, and bases at stands 1 and 2. Its projected position on the x axis is midway between stands 1 and 2.

A second axis can be constructed by the same method using a line on the paper erected at a right angle to the x axis. Two new reference stands are selected which are in close proximity on the x axis, but which are nevertheless separated by a great interstand distance. In the matrix in Table 1, stands 3 and 4 fit such criteria showing an x axis separation of 12 units and an interstand distance of 82.2 units. If stand 3 is assigned a location at its upper arc intersection point in Fig. 1, then the interstand distance of 82.2 units of stands 3 and 4 indicates that the proper location of stand 4 is at its lower arc intersection point (intersection of underlined number 4, Fig. 1.). The location of stands 3 and 4 is shown, in relation to the x axis reference stands, in Fig. 2.

Stands 3 and 4 are, therefore, separated by a projected distance of 12 units on the x axis in Fig. 1, but are, nevertheless, separated as shown in Fig. 2 by an interstand distance of 82.2 units. The x axis proximity of stands 3 and 4 and their high spatial separation indicate that they might be used

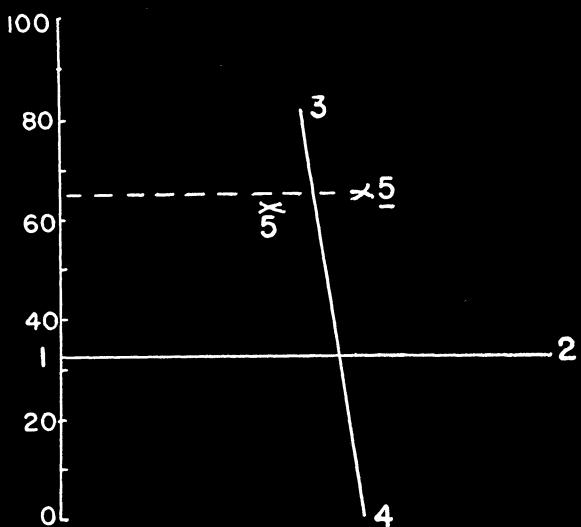


FIG. 2. Demonstration of y axis construction and stand location. Stand 5 is located at one of the two intersections of arcs 20.4 units from reference stand 3 and 64.8 units from reference stand 4. The distance of 50 units from stand 2 to stand 5 indicates the point of intersection to the right is the correct point for projection onto the y axis.

as reference stands for y axis construction. In Fig. 2, a y axis location of stand 5, which is 20.4 units from reference stand 3 and 64.8 units from reference stand 4, is illustrated. The arc intersections of stand 5 with reference stands 3 and 4 shows, after projection, two separate y axis locations, one of which, because the line connecting stands 3 and 4 is not perpendicular to the x axis, is incorrect. To determine the correct position of stand 5, the distance of stand 5 from the reference stands of the x axis should be consulted. The distance of stand 5 from reference stand 2 is 50 units which indicates that the arc intersection to the right (intersection in Fig. 2 with underlined no. 5) which is 50 units from stand 2, is the correct point for projection onto the y axis. Stand 5 is located, therefore, after perpendicular projection at a distance of 65 units on the y axis in Fig. 2.

By following the outlined technique, the information on interpoint distances in Table 1 has been used to indicate the spatial location of the points in a two-dimensional ordinate system. If such distance information necessitated the use of more than 2 dimensions, then further dimensions could be constructed, using the same technique.

APPLICATION OF THE METHOD

X AXIS CONSTRUCTION

The ordination of the upland forests depends upon selecting stands from the complete matrix which can be used as reference points for the location of the other stands. Since the available interstand distances in the complete matrix represent only proximate distances, it is obvious that any resulting stand ordination will only approximate interstand relationships. It is assumed, however, that there is a certain degree

of order within the matrix and that the interstand distances are not a series of random numbers. Only a limited number of stand positions for any one stand should, therefore, be possible. As noted before, these positions should fluctuate within a narrow area if an ordination is to present a meaningful approximation of the matrix measurements.

Before the reference stands for the first axis can be selected, coefficient of community values, as found in the complete matrix, must be inverted so that a low coefficient of community value represents a relatively greater spatial separation and a high value represents a close proximity. Although the coefficient has a range from 0 to 100, the error involved in sampling a stand makes it unlikely that any of a series of replicate samples from the same stand will show the maximum value. Two stands were sampled, each 7 times, using the field methods described earlier, and coefficients of community were calculated among these samplings. The mean coefficient of community within each of the 7 replications was 82 which indicated a mean error of index reproducibility of around 20 index units. A value of 80 was, therefore, considered to represent the maximum coefficient value, that is, the value for two identical stands; the highest value actually found in the complete matrix for 59 stands was 79.

To convert coefficients of community to interpoint distance values, an inversion was accomplished by subtracting each coefficient value from the fixed maximum of 80. Stands which had a coefficient of 0 were separated, therefore, by a maximum distance of 80 units. All subsequent mention of stand interpoint distances refers to the inverted coefficients of community.

Using the criterion of the greatest spatial separation for the choice of reference stands, an examination of the inverted values showed 3 pairs of stands, numbers 35 and 136, 00 and 137, and 33 and 138, to be separated by the maximum distance of 80 units. Since these 3 stand pairs each showed coefficients of community of zero indicating no similarity, their relationship to the other stands in the study was examined to determine whether they were completely unrelated to the other stands. It is suggested that a stand pair with a 0 coefficient of community be used as a reference pair only if each member of the pair shows a value greater than 0 with all stands which are not members of reference pairs. By establishing this criterion, the choice of a stand pair member which shows no relationship to other stands, and which, therefore, contributes nothing to a knowledge of their relative spatial location, will be avoided. This criterion can be met in relation to stand pairs 35-136, 00-137, and 33-138 each member of which shows a relation greater than 0 to every other stand in the study.

The stand pairs selected above appear to represent 2 sets of related stands, numbers 136, 137 and 138 and numbers 00, 33, and 35. The index values between each of the members of each set were highly

significantly correlated, as tested with r . Each of the 3 pairs of reference stands were used, therefore, to ordinate stands along the x axis on the supposition that the use of several sets of stand data might include more information from the matrix than if a separate set were used, and might reduce the fluctuations from non-exact distance measurements.

Since each of the 3 pairs of reference stands were separated by the maximum distance of 80 units, a line of 80 units was drawn connecting each of the reference pairs. The ordination was accomplished by the technique outlined above of arc rotation and of the projection of the point of arc intersection onto the x axis. Stand 89, for example, showed a coefficient of community of 39 and 17 with stands 00 and 137. The inverse of these values, representing spatial separation, is 41 and 63, and stand 89 was located, therefore, at the intersections of arcs with radii of 41 and 63, respectively. These intersections were projected perpendicularly onto the x axis at a position of 25.5 units from reference stand 00 and of 54.5 units from reference stand 137.

The final x axis position of a stand was determined as the median position for the stand in relation to the three pairs of reference stands. There was a close similarity in the x axis positions of the stand in relation to the three pairs of reference stands. Stand 89, for example, had x axis positions of 54.5, 48.5, and 46.5, and was assigned an x axis location of 48.5. The final median values presenting x axis location are shown in column 1 of Table 2.

TABLE 2. Stand locations in three dimensions

Stand No.	ORDINATION AXIS			Stand No.	ORDINATION AXIS		
	X	Y	Z		X	Y	Z
00	79.0	35.5	37.0	93	53.0	54.0	52.0
01	55.0	58.5	41.0	95	4.0	45.75	40.5
03	21.0	55.0	32.0	96	37.5	51.75	33.0
04	32.5	61.25	43.0	100	65.0	30.25	48.0
05	63.0	38.0	50.5	101	62.0	21.0	52.0
06	46.5	33.5	41.5	102	49.5	40.75	45.5
09	45.0	38.75	44.0	103	61.0	33.5	48.0
15	67.5	32.75	58.0	104	68.0	41.0	66.0
16	14.0	39.0	19.0	105	28.0	41.0	23.0
17	21.0	56.5	40.0	106	16.5	44.5	14.0
18	20.5	40.75	28.0	107	47.0	55.5	19.5
19	66.0	27.75	57.5	108	43.0	57.5	28.0
20	63.0	39.5	55.0	109	60.0	60.25	21.0
21	17.0	38.25	13.5	110	18.5	57.75	48.5
23	71.0	53.5	50.5	111	47.0	61.75	33.0
24	56.5	59.0	54.0	112	37.0	42.0	50.0
25	68.5	25.0	59.0	114	31.5	70.75	41.0
26	46.5	61.75	30.5	117	27.0	61.0	45.5
31	76.0	35.25	44.5	118	13.5	66.5	53.0
33	74.0	46.25	39.0	119	18.0	72.5	39.0
35	77.0	38.5	32.0	120	19.5	62.0	28.5
41	11.0	39.0	39.0	121	10.5	64.25	41.0
73	14.5	53.75	31.5	127	55.0	45.75	55.5
85	16.5	62.5	47.5	128	61.0	43.75	32.5
86	71.0	43.5	30.0	136	8.5	47.0	30.0
87	42.0	50.5	47.0	137	7.5	36.75	52.0
88	73.5	37.0	57.0	138	7.5	39.0	34.0
89	48.5	49.0	60.5	151	30.5	47.25	43.0
91	70.0	54.25	39.5	185	47.0	17.5	40.0
92	62.5	25.0	61.5

Y AXIS CONSTRUCTION

The choice of reference stands for the second axis is based upon criteria which are, in part, similar to those used in the choice of the first dimension reference stands: stands separated by the greatest interpoint distance and by the least projected x axis distance can be expected, if chosen as reference stands, to give the greatest spatial separation to the other stands. Stand pairs which most closely fit the above criteria are likely to be central in axis location since by the mechanics of the arc intersection and projection technique, the more nearly stands are found toward the center of any axis, the greater is the probability that they will have spatial separation in the new dimension of a relatively great distance. Conversely, stands located towards one of the ends of the axis are less likely to be distantly related, since by sharing a relatively high relationship with the reference stands towards which they are found, they are, therefore, more likely to be related to each other.

A test is suggested for the selection of y axis reference stands in which the value of stand separation on previous axes is subtracted from the index value of interpoint distance, with the highest value considered to be the most suitable. Such a test weights a low separation on previous axes as of equal importance with a high degree of interpoint distance. The importance of choosing reference stands in close proximity on previous axes is illustrated in subsequent z axis construction in which the condition of non-exact interpoint distances makes it impossible to correct for non-perpendicular axes. This test was applied to the 59 stands in the study and stand pair 111 and 185, which are separated by a projected x axis distance of 0 units (Table 2) and by an interpoint distance value of 47 (as inverted from a coefficient of community of 33), gave a maximum value of 47. Another stand pair, 26 and 185, also gave a high value (46.5) by the above test, with separations of 0.5 and 47 respectively. Stands 26 and 111 were found to be highly significantly correlated in their relationship to the other stands, and the use of several reference sets again appeared feasible. Stands 26 and 185, and 111 and 185 were, therefore, selected as y axis reference stands. Since these two sets of stands were separated by only 0.5 and 0.0 units respectively on the x axis, projections after arc rotation were made directly onto the line connecting each reference pair, and this line was considered the y axis. Final y axis location for each stand was determined by taking the mean position for each stand on the two constructed axes. These axis positions are shown in column 2 of Table 2.

Z AXIS CONSTRUCTION

With the completion of the y axis, a search was made for stands which had relatively similar x and y axis positions, but which were, nevertheless, separated by relatively great interstand distances. The same test of maximum axis separation was made

as in the choice of the y axis reference stands, and a pair of stands, numbers 89 and 107 were found to give the highest value. Stands 89 and 107 were separated by an interstand distance of 41 units and by projected distances of 0.5 on the x axis and of 8.5 on the y axis for a test value of 32.5. The line connecting reference stands 89 and 107, although not perpendicular to the y axis and, therefore, not exactly parallel to the z axis was, nevertheless, used as a base line onto which to project the arc intersections. This was necessary since the sampling error involved in the area of uncertainty surrounding each stand made it impossible to apply formulae which would correct the effect of a non-perpendicular axis. This error also prohibited the consultation of distances to the x or y axis reference stands, since some stands to be projected onto the z axis were found to be equidistant from the x and y reference stands. No choice could, therefore, be made (as is illustrated in the location of stand 5 in Fig. 2) between upper and lower intersection points. Arc intersections were, therefore, projected directly onto the line connecting reference stands 89 and 107. The projections onto this line were considered z axis stand locations, and are shown in column 3 of Table 2.

RESULTS

Using the values in Table 2, each of the 59 stands studied was located on a two dimensional graph by the intersection of its values on any two of the three axes. In Fig. 3, for example, each point on the graph

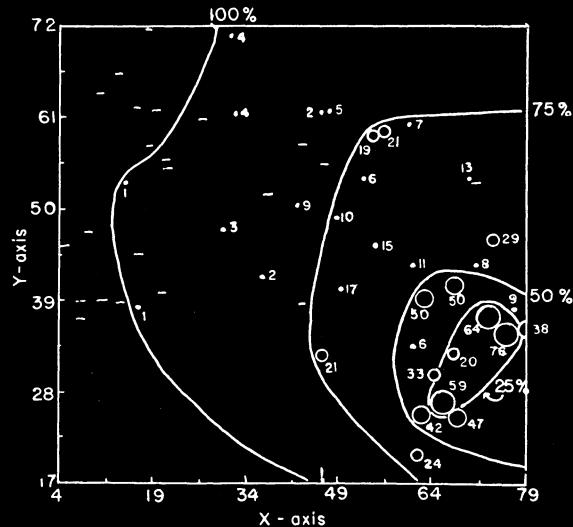
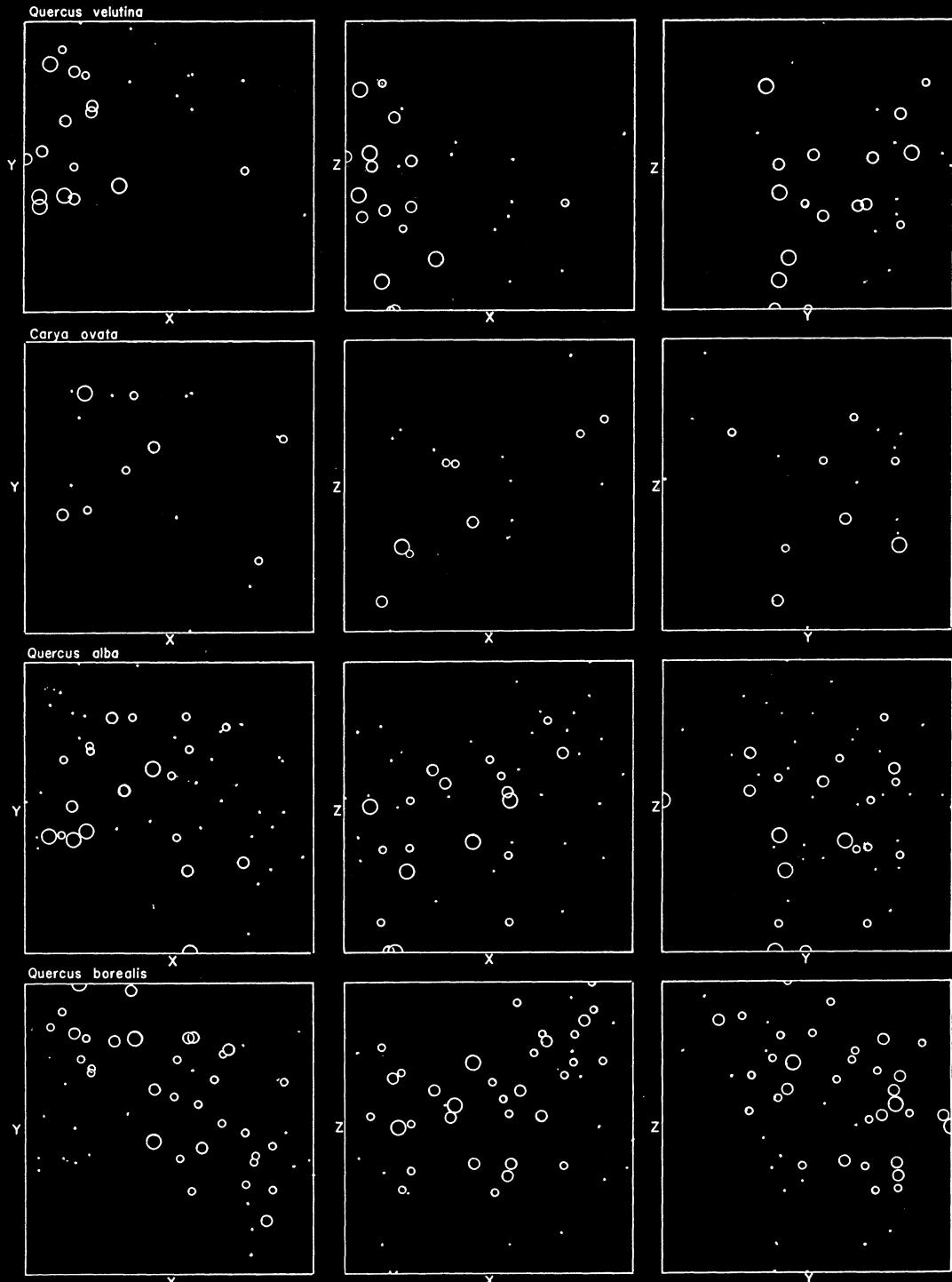


Fig. 3. Demonstration of dominance distribution of *Tilia americana* within the x-y ordination. Each circle or dash represents a stand location. Actual dominance figures in basal area per 100 sq. in. per acre at breast height are given beside each stand location. Values in the upper 25% are represented by the largest circle, values in the 50 to 26% quartile by medium sized circles, values in the 75-51% quartile by small circles, and values in the 100 to 76% quartile by dots. Contour lines are drawn around the 4 quartile lower limits in such a manner as to include all examples of the indicated size class whether or not lesser size class values are present.

represents a stand with its locus determined by its values in Table 2 for the x and y axes. Similar plottings were made for the stand locations on the x and z axes and the y and z axes. These 3 graphs can be thought of as 3 views (front, top, and side) of a three-dimensional cube, within which the stations are located at the intersections of lines projected

from each axis. The actual construction of three-dimensional models is very time consuming (Fig. 7).

Once the stands are located in a two- or three-dimensional configuration, it becomes easy to study the behavior of individual species within the stands. In Fig. 3, for example, the actual basal area per acre for *Tilia americana* is plotted on the x-y



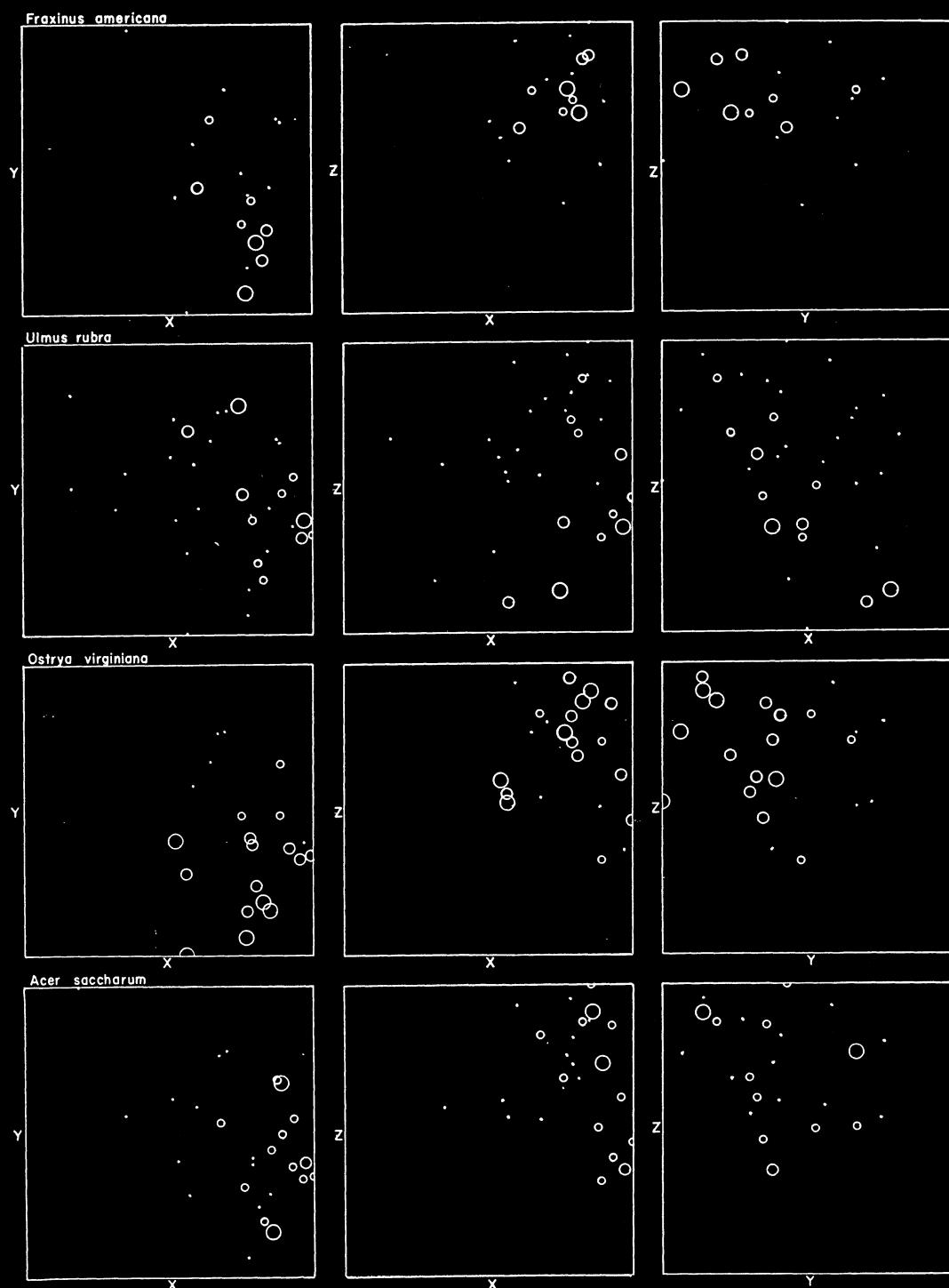


FIG. 4. Dominance behavior of the 8 most important tree species (other than *Tilia americana*) within each of the 3 views of the ordination. Size of circle corresponds to the quartile size class distribution illustrated in FIG. 3. Dominance per acre at the 50% level in sq. in. is as follows: *Acer saccharum* 8,000; *Carya ovata* 1,000; *Fraxinus americana* 2,200; *Ostrya virginiana* 400; *Quercus alba* 5,700; *Quercus borealis* 7,600; *Quercus velutina* 4,000; *Ulmus rubra* 3,200.

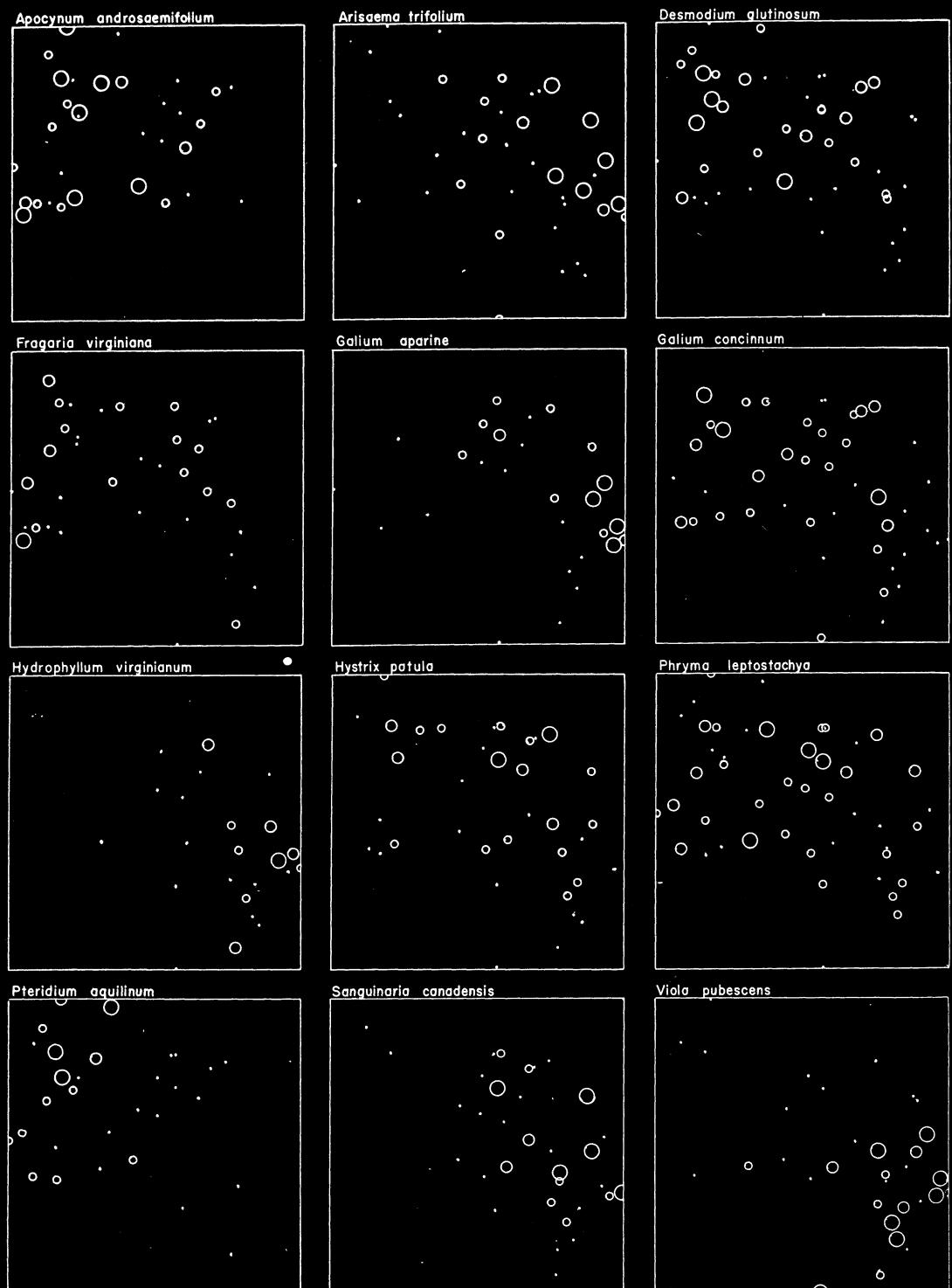


FIG. 5. Frequency behavior of score herbs (12 species) within the x-y ordination. Size of circle corresponds to the quartile size class distribution illustrated in FIG. 3. Frequency at the 50% level is as follows: *Apocynum androsaemifolium* 10; *Arisaema trifolium* 30; *Desmodium glutinosum* 40; *Fragaria virginiana* 25; *Galium aparine* 50; *Galium concinnum* 47; *Hydrophyllum virginianum* 25; *Hystricia patula* 10; *Phryma leptostachya* 30; *Pteridium aquilinum* 27; *Sanguinaria canadensis* 35; *Viola pubescens* 37.

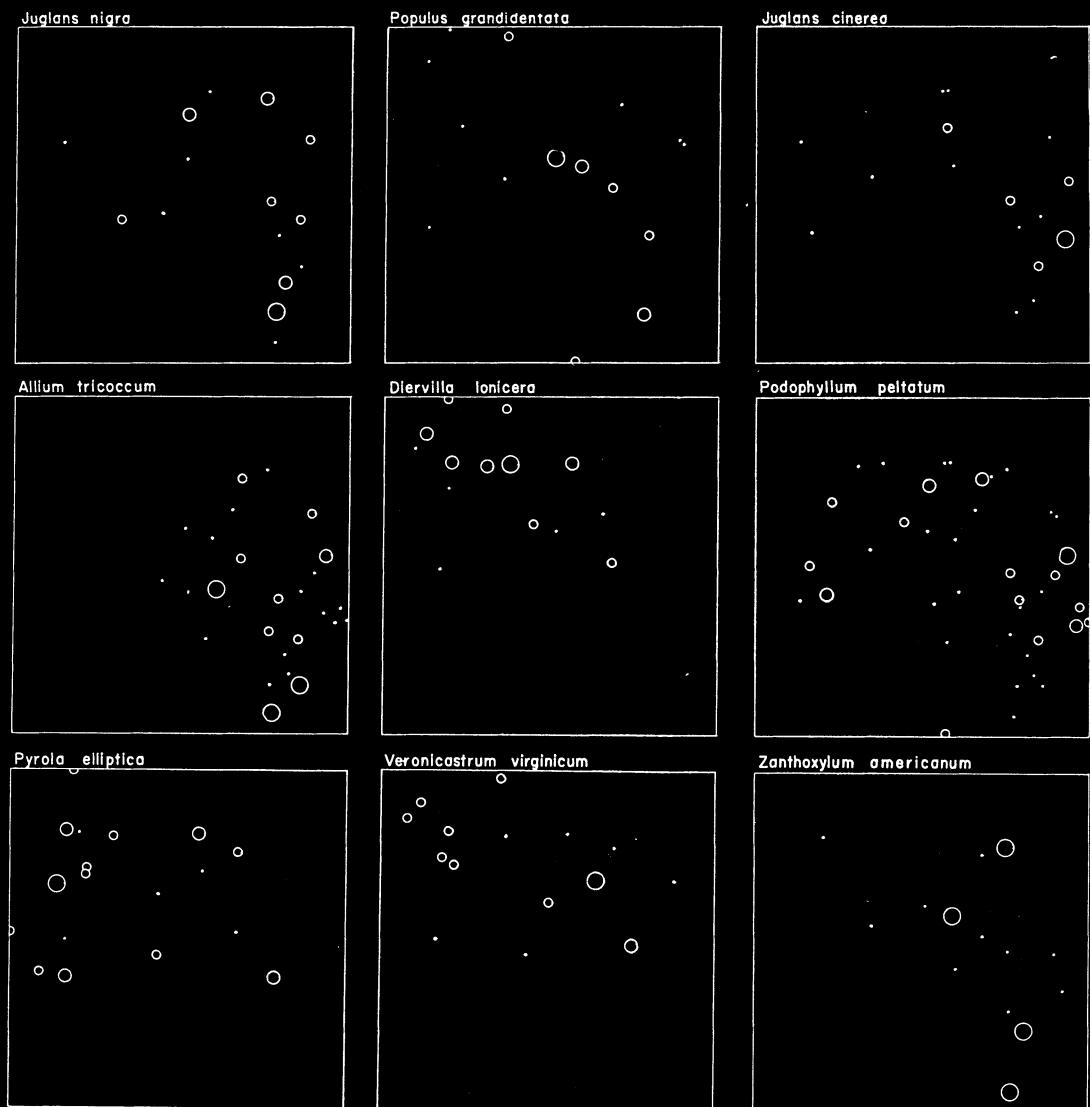


FIG. 6. Frequency behavior (understory species) and dominance behavior (trees) of 9 species not used in ordination construction. Size of circles corresponds to the quartile size class distribution illustrated in FIG. 3. Dominance per acre at the 50% level in sq. in. is as follows: *Juglans cinerea* 2,100; *Juglans nigra* 800; *Populus grandidentata* 1,200. Frequency at the 50% level is as follows: *Allium tricoccum* 10; *Diervilla lonicera* 10; *Podophyllum peltatum* 30; *Pyrola elliptica* 15; *Veronicastrum virginicum* 10; *Zanthoxylum americanum* 20.

graph. The values at each point are the measured basal areas for *Tilia* as taken from the field data for each stand. Those stands in which *Tilia* was absent are indicated by a dash. The basal areas have been put into size classes, as indicated by the circles of different size. In this and all similar figures in the paper, the largest circle includes the top 25% of all of the values; the next size, the third 25%; the smallest circle, the second 25%; and the solid points, the first or lowest 25% of the values. At a glance, therefore, it is apparent that *Tilia* reaches its highest importance in a very small portion of the possible area and that the stands with lesser domi-

nance of this species are spread out from it in a pattern of decreasing occurrence. The contour lines on Fig. 3 have been drawn in such a way as to include all examples of the indicated size class, regardless of whether lesser size classes are also present. They, therefore, indicate the area within which the species may reach the indicated level of domination.

Similar graphs were made for all axis combinations for all species used on the test sheet and for a large number of species not used in the ordination. Fig. 4 illustrates the 3 views for the 8 most important tree species, while Fig. 5 shows x-y views only for

the 12 herbs used on the score sheet. Nine species not used in constructing the ordination are shown in Fig. 6 in x-y views.

A three-dimensional representation of the behavior of *Quercus borealis* is given in Fig. 7. The 3 sizes of spheres indicate the top 3 quartiles of dominance per acre. No differentiation is made between the lowest quartile and the stands not containing the species; both are indicated by holes which appear as dots in the figure. A comparison of Fig. 7 with the appropriate views of *Q. borealis* in Fig. 4 will show how these separate presentations may be used to gain a visual image of the ordinations in three-dimensional space.

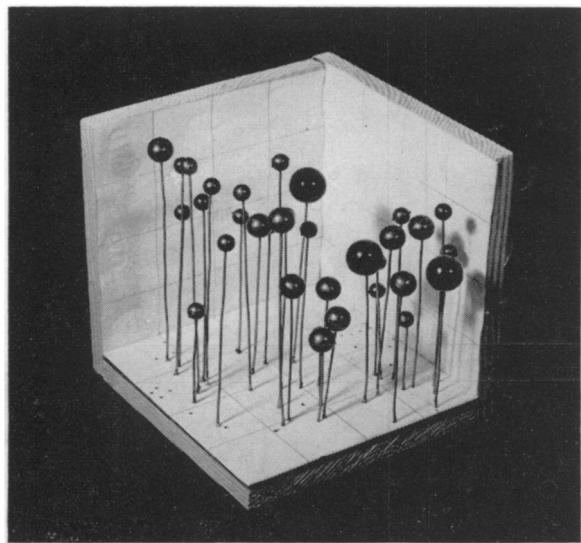


FIG. 7. Three-dimensional model of the dominance behavior of *Quercus borealis* within the ordination. The 3 sizes of spheres indicate the top 3 quartiles of dominance per acre. Stands of the lowest quartile and without the species are represented with holes which appear as dots in the figure. The x axis is on base of model at front from left to right; y axis on base from front to rear; z axis in vertical plane from below to above.

Certain measures of the environment, including soil analyses made upon a pooled sample from 3 random collections of A_1 layer in each stand are given in Table 6 for the stands used in the study. The soil nutrient analyses were made by the State Soils Laboratory, Madison, Wisconsin. Water retaining capacity was determined by the method outlined by Parteh (1949).

DISCUSSION

THE MECHANICAL VALIDITY OF THE ORDINATION

The biologic and environmental results of the ordination in Table 2 should be assessed by criteria which are consistent with the assumptions upon which the ordination technique is based. The first of these assumptions is that the degree of compositional similarity between stands can be used as comparative distances to indicate spatial locations for these stands.

The complexity of stand relationship and of the forces which influence community structure is of such magnitude that a matrix of comparative distance cannot, as previously noted, be oriented in a single exact configuration. The complexity of stand relationship is not chaotic, however, and it is assumed that each stand fluctuates within a fairly limited area in its compositional (and spatial) relationships, although this area is enlarged by the sampling error of the techniques used in field survey. The ordination is further based on the assumption that by establishing a set of exact criteria for stand selection, the number of interdependent causal complexes acting within the community can be limited. This limitation increases the probability that reference stands can be selected which are oriented along the lines of major changes in community structure, but it does not necessarily prevent a certain loss of matrix information by the selection of reference stands which reflect, in part, independent causal happenings which are unrelated to the major complexes. It is evident, therefore, that the validity of the ordination should be tested on its ability to approximate (but not exactly reproduce) the estimates of stand similarity, and perhaps to show stand alignments which correlate with the available estimates of physical environmental features.

TABLE 3. Interstand distances of the reference stands from matrix and ordination. The first column lists all pair combinations of reference stands; second column shows coefficients of community inverted to represent interpoint distance; third column shows distances between the stands in the ordination.

Stand Pairs	Matrix Distance	Ordination Distance	Stand Pairs	Matrix Distance	Ordination Distance
00- 35	16	06	89-107	41	41
00- 33	25	12	89-111	35	30
00- 89	41	40	89-185	46	38
00-107	37	42	89- 26	38	33
00-111	48	42	89-136	64	50
00-185	49	37	89-138	64	49
00- 26	58	42	89-137	63	44
00-136	79	72	107-111	25	15
00-138	78	72	107-185	46	43
00-137	80	73	107- 26	25	13
35- 33	21	11	107-136	57	41
35- 89	55	42	107-138	58	45
35-107	48	37	107-137	70	54
35-111	58	38	111-185	47	45
35-185	55	37	111- 26	21	03
35- 26	55	38	111-136	53	41
35-136	80	69	111-138	65	46
35-138	79	69	111-137	70	50
35-137	79	72	185- 26	48	45
33- 89	52	33	185-136	64	49
33-107	51	35	185-138	61	45
33-111	56	32	185-137	69	46
33-185	63	39	26-136	64	41
33- 26	61	33	26-138	59	45
33-136	77	66	26-137	72	51
33-138	80	67	136-138	42	09
33-137	78	68	136-137	34	24
			138-137	30	18

To assess the approximation of ordination distances to coefficient distances, 58 stand pairs were selected at random and their interpoint distances in the ordination compared with their coefficient of community values in the matrix. Interstand distance between two points (with locations x_1 , y_1 , and z_1 , and x_2 , y_2 , and z_2) was determined by the formula

$$\sqrt{(x_1 - x_2)^2 + (y_1 - y_2)^2 + (z_1 - z_2)^2}.$$

The comparison of the 58 stand pairs showed a correlation value of -0.35 which is significant at the 1% level. The correlation is negative since ordination distance between stands, which shows low values for a high similarity in composition, was compared with coefficient of community values which show high values for a high similarity. The highly significant correlation demonstrates the tendency for the ordination to approximate the stand relationships in the matrix. The check of ordination distance compared to coefficient distance was also applied to the 11 reference stands. Coefficient of community values were first inverted by the method previously discussed to represent degree of spatial separation and are presented in the first column of Table 3. The second column of the table shows interpoint distance in the ordination as calculated by the above formula. The correlation coefficient of these two distances for 55 stand pairs is $+0.73$ which is significant at the 0.1% level.

The test of the ordination as a whole is that it approximates the interstand distance relationships in the matrix of coefficients of community. For any individual axis, however, additional assurance is necessary that it has contributed new and meaningful separations of the stands. A correlation test was, therefore, applied among the stand locations of the 3 axes. Stand locations along the x and y axis and along the y and z axis were found to be uncorrelated. Stand locations on the x and z axis were, however, correlated at the 5% level, though not at the 1% level. It was, therefore, possible that the z axis repeated, in part, information previously revealed in the x axis. It was decided that this repetition was not sufficiently great to justify discarding the z axis for the following reasons: (1) As will be demonstrated, the z axis showed meaningful separations of species midpoint locations which were not available on previous axes. (2) The x-z species distribution patterns in Figs. 4 & 9 showed little tendency toward a linear arrangement which would result if the axes were perfectly correlated. (3) Of 10 environmental measurements which were tested with each axis, 7 were correlated with the x axis, but, of these 7, only 2 were also correlated with the z axis. One of these two correlations was of a ratio which had a different basis on the z axis than on the x axis. There was also an environmental feature which correlated with the z axis, but not with the x axis.

The third test of ordination validity is whether the x, y, and z axes lead to a randomization of stand location. Such a randomization would obscure any differences in species or environmental behavior. It

is apparent that if this were the case, then the species midpoints on each of these axes, as shown in Table 4, would have been in the same location, which they clearly are not. A random unordered stand orientation would probably also result in few or no environmental correlations, but as seen from Table 7, this does not happen. Every environmental feature is correlated with at least one of the axes.

TABLE 4. Location of species midpoints on ordination axes. Midpoints are mean axis locations of dominance values and represent point at which species reaches its optimum importance with respect to size.

Species	X	Y	Z
<i>Quercus macrocarpa</i>	16.3	46.4	38.3
<i>Quercus velutina</i>	17.4	49.3	41.0
<i>Carya ovata</i>	30.1	44.8	29.5
<i>Prunus serotina</i>	31.5	46.5	30.1
<i>Quercus alba</i>	35.5	46.7	32.9
<i>Quercus borealis</i>	40.9	51.8	42.7
<i>Ulmus americana</i>	44.8	33.5	41.9
<i>Populus grandidentata</i>	47.6	45.4	49.4
<i>Juglans nigra</i>	56.6	41.0	43.4
<i>Ostrya virginiana</i>	57.7	34.9	50.4
<i>Fraxinus americana</i>	62.2	31.8	45.5
<i>Juglans cinerea</i>	63.1	40.4	43.7
<i>Carya cordiformis</i>	63.3	43.6	42.7
<i>Tilia americana</i>	64.9	37.5	49.9
<i>Ulmus rubra</i>	67.8	42.9	38.3
<i>Acer saccharum</i>	68.4	40.5	48.8

The determination of species midpoints referred to above was made by finding the mean quantitative behavior (in this case, absolute basal area per acre) in each of 10 equal gradient sections, weighting the mean value by axis position, summing these weighted values, and dividing by the sum of the quantitative behaviors. These midpoint values for dominance per acre are shown in Table 4. They indicate the point at which each species reaches its optimum importance, at least with respect to size.

The differing relationships of species with each other along the 3 gradients can be seen from Table 4. Along the x axis, for example, *Acer saccharum* and *Ulmus rubra* occupy almost identical positions, and both are separated from *Ostrya virginiana* by over 10 units, yet, on the z axis, *Acer* and *Ulmus* are separated by over 10 units, while *Acer* is less than 2 units distant from *Ostrya*. Similarly, *Ulmus americana* and *Quercus borealis* which are less than 4 units distant on the x axis, are separated by over 18 units on the y axis, while *Juglans nigra* and *Ostrya virginiana* which are 1.1 units apart on the x axis, are separated by 6.1 and 7.0 units on the y and z axis, respectively.

The distances between the basal area per acre midpoints of the species is shown, for 3 dimensions, in the upper-right of Table 5. This table can be used as a basis for a spatial ordination of the species which is comparable to the patterns presented in DeVries (1953). A drawing of such an ordination with midpoint locations the same as on the 3 axes of Table 4

TABLE 5. Species midpoints—interpoint distances in three dimensions. The upper-right of the table shows the distances between the dominance midpoints of species in three dimensions. The lower-left indicates whether there was greatest separation of midpoints in the first, second, or third dimension.

	Q.m.	Q.v.	C.o.	P.s.	Q.a.	Q.b.	U.a.	P.g.	J.n.	O.v.	F.a.	J.c.	C.c.	T.a.	U.r.	A.s.
<i>Quercus macrocarpa</i>	4.1	16.4	17.3	19.9	25.6	31.4	33.2	41.0	44.7	48.7	47.5	47.3	50.7	51.6	53.5
<i>Quercus velutina</i>	2	..	17.7	18.0	20.0	23.7	31.7	31.6	40.2	43.8	48.3	46.6	46.3	49.6	50.8	52.3
<i>Carya ovata</i>	1	1	..	2.3	6.7	18.4	22.3	26.5	30.1	36.0	38.1	36.2	35.7	41.0	38.8	43.1
<i>Prunus serotina</i>	1	1	2	..	4.8	16.6	22.0	25.1	28.9	35.2	37.4	34.9	34.3	39.8	37.4	41.8
<i>Quercus alba</i>	1	1	1	1	..	12.3	18.5	20.5	24.2	30.7	33.1	30.3	29.8	32.5	33.0	37.1
<i>Quercus borealis</i>	1	1	3	3	3	..	18.7	11.4	19.1	25.0	29.3	24.9	23.8	28.8	28.7	30.3
<i>Ulmus americana</i>	1	1	1	1	2	2	..	14.3	14.1	15.5	17.9	19.6	21.1	22.0	25.1	25.5
<i>Populus grandidentata</i>	1	1	3	3	3	3	2	..	11.7	14.6	20.3	17.3	17.2	19.0	23.2	21.4
<i>Juglans nigra</i>	1	1	1	1	1	1	1	1	..	9.3	10.9	6.5	7.2	11.1	12.4	13.0
<i>Ostrya virginiana</i>	1	1	1	1	1	1	2	2	3	..	7.4	10.2	12.9	7.5	17.7	12.2
<i>Fraxinus americana</i>	1	1	1	1	1	1	1	1	2	3	..	8.8	12.2	7.6	14.3	11.2
<i>Juglans cinerea</i>	1	1	1	1	1	1	1	1	1	3	2	..	3.3	6.3	7.6	7.3
<i>Carya cordiformis</i>	1	1	1	1	1	1	1	1	1	2	2	2	..	9.6	6.3	8.5
<i>Tilia americana</i>	1	1	1	1	1	1	1	1	1	1	2	3	3	..	13.1	4.7
<i>Ulmus rubra</i>	1	1	1	1	1	1	1	1	1	1	3	2	3	1	3	10.8
<i>Acer saccharum</i>	1	1	1	1	1	1	1	1	1	1	1	2	1	3	1	3

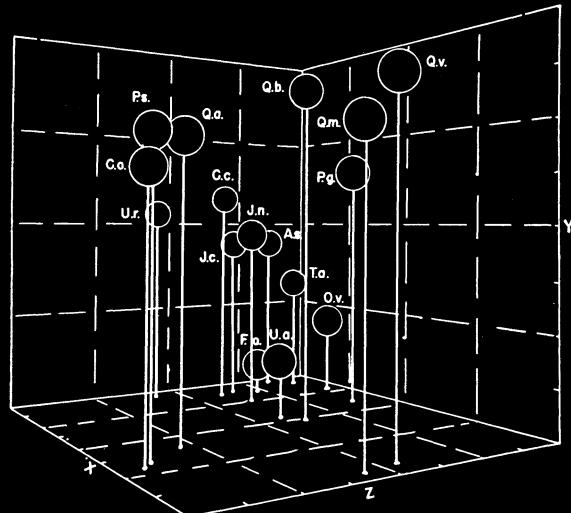


FIG. 8. Three-dimensional drawing of the center point locations of dominance behavior of tree species. Determination of center point locations explained in text. Point on frame closest to reader is lowest value for all 3 axes. The traditional position of the axes was changed to prevent the hiding of some species in the drawing.

is presented in Fig. 8. Both the upper-right of Table 5 and Fig. 8 show community relationships of species by suggesting an estimate of the relative correspondence of their stand locations; the less distant is the degree of midpoint separation, the more likely are the species to occur in the same stands.

The lower left of Table 5 lists the axis for each stand pair on which there is the greatest spatial separation in their dominance midpoints. In spite of the greater importance of the x axis (with a maximum distance between midpoints of 52.1 as compared to 20.0 and 20.9 for the y and z axes), there are 33 of a total of 120 stand pairs which give a greater separa-

tion on the y or z axis than on the x axis. These separations, in many cases, complemented the results of field observations, and gave indication that a biologic interpretation of the meaning of the axes might be possible.

THE BIOLOGIC VALIDITY OF THE ORDINATION

The ordination, therefore, by the use of a technique which is open to modification, gave one (but certainly not the only possible) approximation to the information on stand similarity in the matrix of coefficients of community. This approximation was made in 3 dimensions which were demonstrated to give species locations and environmental correlations which were non-random and non-repetitive. The ultimate test of the value of the ordination is, however, a biologic one, and succeeding discussion will attempt to utilize the ordination in examining the nature of the community and of its factorial relationships.

The views of species distribution in Figs. 4, 5, and 6 can be used in creating a mental image of the species as they appear in three dimensions, an image which will reveal the same effect as that of the 3 dimensional pattern in Fig. 7. From these visualizations and from Fig. 7, it is evident that each species shows all or part of an atmospheric distribution, that is, one in which there is an increasing concentration (number of points) and importance (size of points) of the species as the center of the distribution is reached. Away from the center, the decrease in numbers and sizes of the points is not always uniform in all directions but the species distributions, nevertheless, suggest that an idealized distribution would show a concentration and size of points diminishing outward in all directions from a dense center to an area beyond a sparse periphery where the points no longer occur.

An atmospheric distribution is a form which can be expected from an extension of the frequently expressed concept of ecologic amplitude into more than 2 dimensions. This concept postulates a mini-

TABLE 6. Environmental measurements by stands. Average canopy estimates from a number of stations within each stand. Soil analyses from pooled samples of 3 random collections of the A₁ layer in each stand. Nutrient values in pounds per acre at a soil depth of 7 in.; W.R.C. is water retaining capacity; OM is organic matter.

Stand No.	Percent Canopy	Depth A ₁ (inch)	pH	WRC%	Ca (lbs.)	K (lbs.)	P (lbs.)	NH ₄ (lbs.)	OM%	1/10 Ca
										K
00	96	4.25	7.0	53	6,000	280	50	20	...	3.2
01	99	4.0	7.3	85	185	45	20	1.6
03	65	4.25	5.8	93	4,000	255	60	30	...	0.3
04	70	2.5	6.0	75	50	160	60	45	...	3.5
05	88	5.25	7.0	87	8,000	230	60	20	...	3.2
06	98	3.0	7.0	96	8,000	250	95	30	...	6.0
09	90	2.5	7.4	77	12,000	200	105	20	7.0	...
15	..	3.5	6.0	58	...	180	40	..	6.0	...
16	..	3.0	5.6	36	2,400	100	50	..	5.0	2.4
17	78	1.7	5.7	100	6,000	130	40	40	5.2	4.6
18	..	3.0	7.0	64	...	220	70	6.7
19	..	7.0	6.7	85	9,400	140	50
20	97	8.0	7.2	54	6,000	230	135	20	...	2.6
21	..	3.0	5.4	48	1,100	150	60	0.7
23	..	2.5	6.8	107	10,000	130	60	..	9.0	7.7
24	..	4.0	5.4	67	4,000	180	40	..	4.0	2.2
25	97	3.5	6.0	71	600	155	130	40	8.5	0.4
26	88	2.25	6.2	93	5,000	200	75	20	...	2.5
31	87	3.25	7.3	75	10,000	430	200	10	...	2.3
33	97	6.0	7.4	66	10,000	370	80	30	...	2.7
35	88	3.5	6.1	75	5,000	190	70	10	...	2.6
41	82	1.5	4.9	79	3,000	260	50	25	...	1.2
73
85
86	98	5.0	6.9	57	5,500	185	60	15	...	3.0
87	85	..	6.2	53	5,000	190	70	30	...	2.6
88	98	..	7.7	83	10,000	130	30	10	...	7.7
89	..	6.0	8.0	42	11,000	250	4.4
91	..	1.0	..	107	..	240	9.0	...
92	38	13.5	5.7
93	..	1.0	6.0	125	15,000	260	4.0
95	70	1.5	7.0	68	3,400	240	50	..	6.5	1.4
96	..	0.5	5.8	79	2,300	160	11.5
100	..	3.0	7.0	94	15,000	180	8.3
101	..	1.5	7.0	94	7,000	160	7.5	4.3
102	..	4.0	6.3	72	..	60
103	95	2.5	7.0	67	6,000	205	10	20	5.5	2.9
104	94	3.0	6.9	61	6,000	190	60	10	..	3.2
105	72	1.0	7.1	66	4,500	185	60	25	5.5	2.4
106	92	3.0	7.0	68	5,000	190	80	25	5.5	2.6
107	..	2.0	5.5	56	1,000	150	2.5	0.7
108	..	5.0	5.7	56	6,200	265	75	60	..	2.3
109	80	3.5	7.4	84	8,000	340	80	35	..	2.4
110	85	3.0	6.5	60	8,000	200	60	25	..	4.0
111	..	0.5	5.5	67	1,300	140	2.0	0.9
112	85	1.25	6.0	85	1,500	180	60	50	..	0.8
114	6.0	123	4,200	320	12.5	1.3
117	80	3.5	7.1	134	10,000	270	80	25	..	3.8
118	83	3.0	6.4	113	7,000	205	60	20	15.0	3.4
119	65	1.5	6.9	139	6,000	250	30	20	..	2.4
120	68
121	..	1.0	6.5	74	5,000	170	6.5	2.9
127	..	4.0	..	107
128	..	1.0	..	162
136	..	5.0	7.1	89	8,000	185	20	15	..	4.3
137	71	1.5	5.5	54	2,000	180	30	15	..	1.1
138	..	1.0	5.6	81	6,000	180	40	30	..	3.3
151	..	1.5	5.3	133	6,000	180	30	35	..	3.3
185	..	0.25	5.8	88	5,000	180	40	15	..	2.8

mum, optimum, and maximum behavior for each species in relation to the dynamics of community structure, and has often been demonstrated in 2 dimensions by contour-shaped ("solid normal") patterns and in one dimension by bell-shaped ("normal") patterns. It can be shown that a compression of an atmospheric distribution into 2 dimensions will give contour-shaped patterns as shown in Fig. 3 and in Wiedemann (1929), Ramensky (1930), Pogrebñjak (1955), and Whittaker (1956). Further compression into one dimension will yield the bell-shaped patterns demonstrated in the original linear treatment of the upland forest (Curtis and McIntosh 1951).

Fig. 6, which shows species patterns similar in form to the two preceding figures, demonstrates the relevance of the ordination to the entire plant population of the upland hardwoods. The 9 species in Fig. 6 include all of the minor tree species for which adequate data were available and an unbiased selection of shrub and herb species. Although none of the species in Fig. 6 contributed to the placement of stands in the ordination, they, nevertheless, show the same atmospheric distributions outlined above. The ability of the ordination to give meaningful patterns to species not used in its construction is considered as both a basic test of the usefulness of the ordination and as a demonstration of the feasibility of gradient construction by the consideration of less than the total species complement.

Figs. 4 through 6 show each species to have an individual pattern, different in size and location, although fairly similar in shape to those of other species. The distribution and the relationship of the patterns within the ordination is clearly one of continuous variation, as was previously demonstrated in the linear continuum of Curtis and McIntosh. The species used in the ordination, as well as those in Fig. 6 which were examined after the ordination was completed, can be described, therefore, as having patterned, non-random distributions within the prescribed geographic, environmental, and physiognomic limits of the study. Each of these distributions moves outward from central areas of high density to peripheral areas of sparse density, and this movement reveals along 1, 2, or 3 dimensions corresponding bell-shaped, contour-shaped, or atmospheric distributions. Each species has a separate area of location, and within this area its distribution is interspersed to varying degrees with other species distributions so that there is a continuous change in stand composition from any part of the ordination to any other part.

The above description supports, to a large degree, conclusions from work completed in a diversity of geographic regions and vegetations, including the studies of Gleason (1926), Vorobyov & Pogrebñjak (1929), Ramensky (1930), Sörenson (1948), Sjörs (1950), Curtis & McIntosh (1951), Whittaker (1951), deVries (1953), Goodall (1954a), Guinochet (1954), Webb (1954), Churchill (1955), Horikawa & Okutomi

(1955), Poore (1956), and Hewetson (1956). It is suggested that evidence for the individualist theory of species distribution and for the continuum nature of community structure is now sufficiently compelling to require studies concerned with community structure to examine the relative continuity or discontinuity of their material and to use quantitative methods which will permit this examination. At a minimum, the examination would include a sampling of at least one analytic character in a sufficient number of stands to allow comparisons of quantitative composition. If an apparent grouping of stands into a discrete unit (i.e. association, etc.) is suspected, then this unit should be tested against samples of related vegetations to determine whether there are separate groups of stands with a certain range of variation within each group, or whether this variation is great enough to obscure the boundaries between the groups. If the latter is true, the application of ordination methods is necessary. A reasonable approach to the treatment of phytosociologic material about which little is known might be to check carefully the homogeneity of each stand, and then to apply an ordination technique. If clumps of stands are shown along the resultant gradients, it would then be possible to regard these clumps as castes (associations, etc.) and determine the suitable parameters necessary for the future classification of each caste.

One reason for reexamining the upland hardwoods of Wisconsin was the diversity of interpretations which various readers gave the original paper. Thus, some correspondents questioned if the linear continuum was not a statistically advanced restatement of succession, while others (Horikawa & Okutomi 1955) regarded it as a demonstration of relationships which were independent of succession. The continuous compositional variation which was demonstrated was at times assumed to apply to spatial transition as seen in the field (Churchill 1955), as contrasted to theoretic variation in the structure of communities regardless of their microgeographic relationships. In clarification of the above interpretations, it should be evident from the present study that the dimensions of the ordination are purely compositional and cannot necessarily be directly related to factors or to complexes of factors. Successional change is only one among many causal forces which have shaped the species distribution patterns of Figs. 4 through 6. The dimensions represent an approximation of the changes in compositional structure which are present within the community and are not spatial transitions as they exist in the field, although, as noted by Gleason (1926) and as is evident to many field workers, there are often natural areas where the salient features of a continuum can be observed.

THE NATURE OF THE GRADIENTS

It is likely that the degree to which there are separations in more than one dimension was in part dependent upon the qualifications used to differentiate the community initially. Had sufficient knowledge

been available before the study was begun, it might have been possible to eliminate those stands from the study which had relatively poor subsoil drainage and one of the additional dimensions might, thereby, have been eliminated. On the other hand, had there been an expansion of the data to include poorly drained forests and those subject to inundation, then a more complete picture of the southern forest as a whole could have been given. The view of Ashby (1948), that the most important aspect of community study is the original delineation of the study area, is very applicable to the present study.

As previously noted, the 3 dimensions of the ordination represent compositional gradients which are not likely to be related to any single causal agency. The probability that every factor is a constant influence on the structure of a stand, and the interrelated nature of biotic and physical factors, prohibits the identification of single causal mechanisms. In spite of these limitations, however, certain over-all patterns are evident in the 3 axes, patterns which relate to broad bio-physical complexes and to history. It is noteworthy that some of these patterns of species and of environmental features had not been suspected before the application of multidimensional technique.

Thus, in general, the x axis duplicates the original linear continuum of Curtis & McIntosh and shows a complex of conditions which include gradients from higher to lower light intensity and evaporation, gradients from lower to higher soil moisture and relative humidity, and gradients from more to less widely fluctuating soil and air temperature. The order of species along the x axis is basically determined by an over-all linear direction in the many paths of community development within the upland forest. These paths follow a network of successional patterns which are mainly related neither to primary nor secondary succession but to recovery from past disturbance. This disturbance, in the form of fire, reduced the forest in many places to a savanna or barrens condition in which there were scattered oaks and/or oak brush and roots (Cottam 1949; Bray 1955). During this reduction, the more terminal species which were also the more fire susceptible, were replaced by less terminal and by initial species which were the least fire susceptible. The coincidence that *Quercus macrocarpa* is both the most initial and fire resistant species, and that *Acer saccharum* is the most terminal and fire susceptible

species, suggests that the ultimate explanation for the composition of a forest stand in upland Wisconsin is largely an historic one. The longer a stand has been free of fire (and other disturbance forces) and the more favorable the habitat in which it occurs, the more likely it can develop to a maple-basswood forest. The x axis shows, therefore, mainly the relationship of the community to major past disturbance factors and to its own developmental recovery from these factors.

To examine correlations with physical measurements of the environment, a check was made, using r , the correlation coefficient, of all available environmental data with each of the three dimensions. The results are shown in Table 7. Since both environmental data and stand locations showed approximately normal distributions, the significance of correlation was checked with the t test by examining the hypothesis that correlation (ρ) = 0. The values in Table 7 are the probability that $\rho = 0$, and that there is, therefore, no correlation. Thus, a probability of $<.01$ is a basis for rejecting the hypothesis and is considered a highly significant correlation. A value of $<.05$ is considered a significant correlation, while values of $>.05$ are considered to represent no significant correlation. By the above interpretation, for example, percent canopy is positively correlated with the x axis at a highly significant level, while it is not correlated with either the y or z axis.

The values in Table 7 show a highly significant correlation between percent canopy, depth of A_1 , organic matter, pH, Ca, P, $\frac{.1\text{Ca}}{\text{K}}$ and the x axis. Water re-

taining capacity, K and NH_4 are not, however, correlated with the x axis. An examination of the values in Table 6 indicated the majority of the features related to the x axis, were positively correlated with each other. It is highly probable that these correlations represent the measured aspects of an increasingly mesic environment which accompany the successional recovery of the forest from past disturbance. While only a general interpretation can be made of this recovery at present, it is clear that the dynamics of factorial interrelationships along the x axis offer a broad area for future research.

The y axis seems to be correlated, in part, with the influence of surface and sub-surface drainage, and, consequently, with a soil moisture complex, with internal soil air space and aeration probably also

TABLE 7. Environmental correlations with three ordination axes. A_1 is depth of A_1 in inches; W.R.C. is water retaining capacity; O.M. is organic matter; Values in body of table are the probability that there is no correlation.

	Percent Canopy	A_1	pH	W.R.C.	Ca	K	P	NH_4	O.M.	$\frac{.1\text{Ca}}{\text{K}}$
x.....	+ <.001	+ <.01	+ <.01	>.05	+ <.001	>.05	+ <.001	>.05	+ <.01	+ <.001
y.....	>.05	>.05	>.05	+ <.001	>.05	>.05	>.05	+ <.01	>.05	>.05
z.....	>.05	>.05	>.05	>.05	>.05	- <.05	>.05	>.05	+ <.05	+ <.01

influential. The 3 tree species with midpoints towards the lower end of the y axis in Table 4 are *Fraxinus americana*, *Ulmus americana*, and *Ostrya virginiana* and are, of the species occurring in the upland forests, the most tolerant of poor drainage and aeration. Species which are found toward the upper end of the y axis are predominantly oaks, such as *Quercus borealis*, *Q. alba*, *Q. macrocarpa*, and *Q. velutina*, which are intolerant of inundation and poor aeration. Species with midpoints towards the center of the axis, such as *Acer saccharum*, *Juglans nigra*, *Ulmus rubra*, and *Carya cordiformis* are mesic species with an intermediate tolerance of poor drainage and aeration.

Two environmental features, W.R.C. and NH_4 show a highly significant positive correlation with the y axis. Water retaining capacity is represented with its highest values occurring towards the upper end of the axis assumed above to have the better internal drainage. The anomaly of high W.R.C. associated with good drainage is perhaps explained by the differences in past history of the stands along the y axis. It was found that W.R.C. has a significant negative correlation with depth of the A_1 layer. This correlation is apparently related to the circumstance that stands with high water-retaining capacities have a sharply demarcated boundary between the A_1 and A_2 layers, while the opposite stands tend to have a diffuse boundary, with the organic matter gradually decreasing in amount. These differences represent trends towards mor humus and typical podzols on the one hand and mull humus and gray-brown podzolic or brown forest soils on the other. They probably reflect past history to the extent that stands at the upper end of the y axis (mor humus, high W.R.C.) have been occupied by mixed conifer-hardwood forests in more recent postglacial times than stands at the other end, which may have developed on savannas or grasslands with a deep layer of incorporated humus. Substantiating evidence for this was seen in the distribution patterns of *Diervilla lonicera*, *Goodyera pubescens*, *Maianthemum canadense*, *Pteridium aquilinum* and *Pyrola elliptica* which closely matched the distribution of the higher values of water retaining capacity. All of these species currently reach their optimum in the conifer forests of northern Wisconsin and are only incidental members of the southern forest under discussion. The mean W.R.C. in stands in which 3 or more of the above species occurred in the quadrat samples is 103 as compared to a mean of 78 for the remaining stands.

The strong positive correlation of NH_4 with the y axis is not related to pH, since these two features show no correlation with each other. There is, however, a likelihood that the NH_4 correlation is, in part, controlled by the soil moisture and aeration complex discussed above in relation to tree distribution. The assumed poorly aerated soils towards the lower part of the y axis have, perhaps, a relatively higher proportion of denitrifying bacteria. With an in-

crease in internal drainage and in soil oxygen along the y axis, there is a proportional increase in nitrifying bacteria and, therefore, an indirect increase in NH_4 . The y axis, therefore, appears to represent a complex of internal soil drainage and aeration factors which is coincident with a clinal historic factor reflecting post-glacial vegetational changes.

The z axis apparently represents, in part, the influence of recent disturbance, with species which benefit by disturbance being separated from the species with which they are proximate on other axes. Both *Carya ovata* and *Prunus serotina* at the lower end of the z axis are gap phase species (Watt 1947, Bray 1956b) which take advantage of oak wilt gaps and of grazing in initial forests. *Populus grandidentata* is another gap phase species and is found toward the upper end of the z axis. Its ability to enter areas opened by fire has long been noted (Chamberlin 1877) and observed in the field. *Ulmus rubra*, and to a lesser extent *Carya cordiformis*, apparently do well in some disturbed intermediate and early terminal forests and, as a result, are pulled away from their proximity to *Acer saccharum* to which they are closely adjacent on the previous axes. *Quercus alba* and *Quercus borealis* are separated on the z axis to a greater extent than on the x or y axes, a separation which might be related to the ability of red oak to increase in importance in maple-basswood forests which have been burned, forests from which white oak had been eliminated earlier by successional developments.

The values in Table 7 show 3 environmental features, K, O.M., and $\frac{\text{Ca}}{\text{K}}$ to be correlated with the z axis. Potassium shows a significant negative correlation which might be related to amount and content of loess, in that K is characteristically high in loessial soils in the Middle West and stands towards the upper end of the z axis might have an increasingly shallow or absent loessial layer. The highly significant positive correlation between the ratio $\frac{\text{Ca}}{\text{K}}$ and the z axis is illustrated by values which more than double from one end of the axis to the other. This correlation is the result of a Ca content which is not correlated along the axis coupled with the decreasing K content noted above. There is, therefore, a consequent increase in the ratio. Along the x axis there is a similar $\frac{\text{Ca}}{\text{K}}$ correlation, but it is produced by an uncorrelated K content which is accompanied by an increasing Ca content. No connection is directly apparent between this ratio and the growth of plants although it may reflect amount of available K. Thus, availability of K is considerably decreased with increased Ca, if K is tending toward low levels of fertility (Lutz & Chandler 1946). Such low fertility levels are possible in the decreasing K concentration along the z axis which is accompanied by a uniformly high Ca level. A similar non-availability

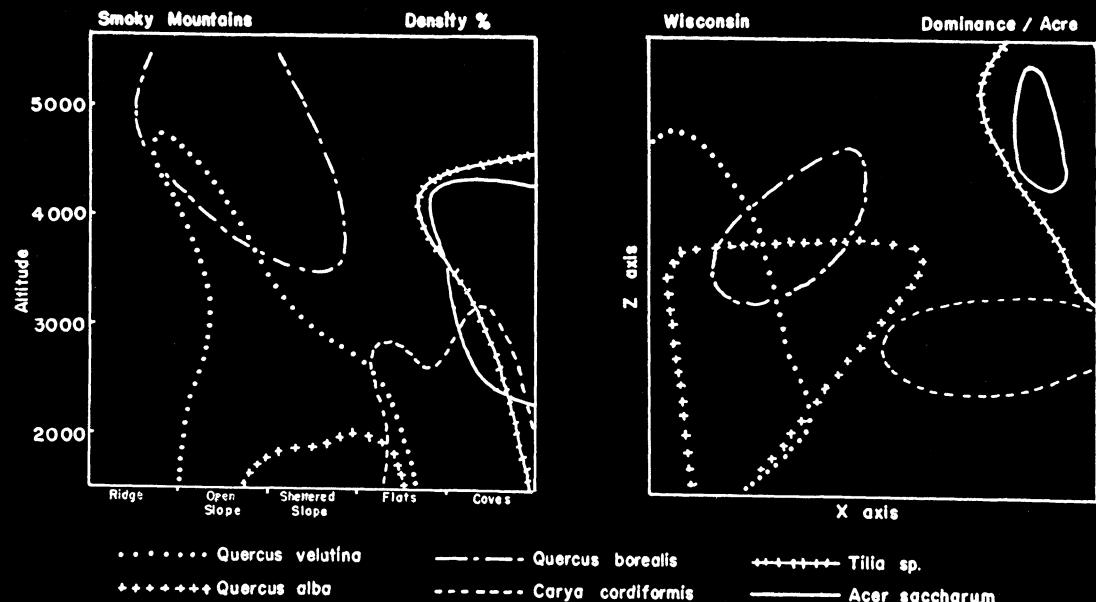


FIG. 9. View of contour drawing of trees within the x-z ordination compared with nomograms of the same or similar species in the Smoky Mountains (Whittaker 1956). Contour lines in the Wisconsin ordinations are made at the 25% (upper) size class level. Dominance values at this level in sq. in. are as follows: *Acer saccharum* 12,000; *Carya cordiformis* 400; *Quercus alba* 8,500; *Quercus borealis* 11,400; *Quercus velutina* 6,000; *Tilia americana* 5,700.

of K correlated with the x axis is not as likely, since the non-correlated K concentration along this axis indicates there is no area where low K values are consistently found with high Ca values.

The reasons for the significant positive z axis correlation with organic matter are not readily apparent. The overwhelming probability that all the measured environmental factors plus numerous non-measured factors are interacting with each other and with biotic forces, and that plants are responding to the interactions rather than to single factors indicates that attempts to pinpoint the axes too closely are doomed to failure.

The difficulty of assigning definite factorial meanings to the ordination axes is further emphasized by a consideration of Fig. 9. This represents a comparison of the two-dimensional behavior patterns of a series of tree species which occurred in the Wisconsin study and also in Whittaker's 1956 analysis of the Great Smoky Mountains vegetation. The species of *Tilia* are slightly different in the two regions. The patterns on the Great Smoky graph are taken from Whittaker's nomograms. They portray either the 10% contour of species density or the highest value attained by the species if it was less than 10% and thus represent favorable or optimum conditions for growth. The patterns on the Wisconsin graph are the contours of the top quartile of dominances per acre. The absolute levels in square inches per acre for this 75% level are indicated in the legend of the figure. This may seem an unfair comparison since only selected contours are used, but a study of the full set of curves in Whit-

taker's original graphs in relation to the full diagrams for the Wisconsin data only strengthens the comparison.

With the exception of *Quercus alba*, the patterns in the two graphs are remarkably similar, especially if the axes of the Wisconsin graph are rotated slightly to the right. The exact meaning of this coincidence is not clear. A relationship between the x axis and Whittaker's moisture gradient seems reasonable enough, but there is no immediately evident connection between the factors usually associated with elevation and any possible interpretation of the z axis. All of the stands in the Wisconsin study were within a few hundred feet of each other in elevation and did not differ significantly in average temperature as measured by nearby weather stations.

The similarity in species distribution patterns between Wisconsin and Tennessee suggests that the biotic forces within a community have a high degree of homeostatic stability in their interactions with other causal agencies. Such stability is a feature of the dynamics of open systems in which, although a wide variety of factorial configurations may exist, there are apparently only a limited number of system structures which are possible. In biotic communities a limitation in structure means each species is confined to a definite community position in relation to other species with the unlikelihood that all combinations of species can occur. It is the limited number of stand compositions which permits the application of quantitative methods to community classification.

FURTHER USES OF THE ORDINATION

Although the main purpose of the study was to investigate the phytosociology of community structure, the ordination results can be used as a basis for further research and for investigations in related fields. The value of the original upland hardwoods continuum in animal ecology (Bond 1955) and in plant ecology (Tresner, Backus & Curtis 1954; Gilbert & Curtis 1953; Hale 1955) has been demonstrated. The construction of additional dimensions should facilitate any further work which is done by providing a more complex pattern of community structure. Thus, studies of life histories of individual species can be given an exact community background against which to correlate those changes in the morphology, vitality, manner and means of dissemination, and perhaps taxonomy and phenology of the species which are determined by differences in community composition. Other important phytosociologic features which can be directly related to differences in community structure are (1) the distribution patterns of species, both as to variation in population means and in manner of dispersion, as demonstrated in Whitford (1949) and (2) the variation in interspecific association relationships.

The nature of the causal role of factors shaping a community is an ultimate goal in ecology. The determination of community structure, as was suggested earlier, is perhaps a key to these causal relationships. Goodall (1954b) notes, "It is the high correlation between different environmental factors that often suggests a deceptively simple relationship between plant distribution and the environment. There is much to be said for the view that the complexes of environmental factors determining plant distribution can be indicated and measured better indirectly, through the plants themselves, than by direct physical measurements; this is, of course, the idea behind the use of "phytometers" in agricultural meteorology, and the attention devoted to phenology." By separating unlike stands along several different compositional gradients, possible extremes in causal reactions are determined and the location of crucial junctures of change in community structure is possible. Elaborate and expensive tests can then be made at these junctures which would have been impossible to apply to the community as a whole. A further interpretation of the southern upland hardwoods would then, perhaps, be able to demonstrate the interactive nature of a series of factors as they change the structure of the community and, in turn, are changed in their own expression.

SUMMARY

The relationships of 59 stands of upland hardwood forest in southern Wisconsin were studied by means of a new ordination technique. Quantitative measurements of 26 different species were used as the basis of the ordination. These 26 species included the 12 most important trees and 14 herbs and shrubs. The quantitative characters used were absolute density

per acre and absolute basal area per acre for the trees and simple frequency for the herbs and shrubs. These measurements were arranged on a "score" sheet for each stand after having been put on a comparable and relative basis. The degree of phytosociologic similarity of any stand to each of the other stands was assessed by Gleason's coefficient of community. Such coefficients were calculated for each stand with each other stand (1711 values).

It was considered that the degree of similarity of two stands as shown by their coefficient could be translated into a spatial pattern in which the inverse of the coefficient was equated with linear distance. Using groups of stands which were least similar as end points of an axis, the relative positions of all other stands were located along this axis by a geometric technique of arc projection, with the radii of the arcs given by the inverted coefficients of similarity. When this was done, it was seen that some stands were equidistant from the two end groups but nevertheless were themselves unlike. Using the most distantly related of these, a second axis was erected by the same method as the first. The position of all stands on this new axis was then determined. Further inspection revealed that a few stands were about equally spaced between the ends of both the new axis and the first axis but were still dissimilar. These were used to produce a third axis. The three axes were at right angles to each other, so the positions of any given stand on each axis could be projected to give a three-dimensional locus for that stand. When all stands were thus located in three-dimensional space, a highly significant correlation was found between their actual, measured spacings and the original coefficient of community values between them.

Given the framework of the spatial distribution of the stands, the behavior of individual species was readily examined by plotting a measured phytosociologic value of a species at the loci of the stands of its occurrence. It was found that all species (including an unbiased selection of those not used in the original 26 on which the ordination was based), formed atmospheric distributions with high or optimum values in a restricted portion of the array, surrounded by decreasing values in all directions. No two species showed the same location, but each was interspersed to varying degree with other species, in a continuously changing pattern.

The three axes of the ordination are compositional gradients, and their structure is interpreted as not the result of a causal determination by the physical environment but of an interaction between organisms and environment. A preliminary attempt was made to describe patterns of this interaction although an exact description remains for future study. Thus, the major (x) axis appeared to represent, in part, patterns of developmental recovery from major past disturbances. This recovery was correlated with features of an increasingly shaded and mesic environment including canopy cover and the following soil features: depth of A_1 layer, organic matter, pH,

Ca, P, and $\frac{1}{K}$ Ca. The second axis was related, in part, with surface and subsurface drainage and with soil aeration and it showed correlation with soil water retaining capacity and NH_4 . The third axis was apparently related to recent disturbance and the influence of gap phase replacement, and it showed correlation with the soil features of $K, \frac{1}{K}$ Ca, and organic matter.

The possibility that the axes may have different interaction patterns than suggested above is evident in the similarity between the two-dimensional distributions of a number of tree species in the Wisconsin stands and in Whittaker's Smoky Mountain stands which were arranged along topographic and altitudinal gradients.

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